植物分类与资源学报 2015, **37** (3): 327~338
Plant Diversity and Resources DOI: 10.7677/ynzwyj201514110

西双版纳布龙自然保护区勐宋片区附生维管植物多样性与分布特征*

赵明旭[1,2,3], Geekiyanage Nalaka[4,5], Harrison Rhett Daniel[1,3]**, 许建初[1,3], Khin Myo Myo[6], Ridwan Nurdiana Dian[7], Paudel Ekananda[1,2]

(1 中国科学院东亚植物多样性与生物地理学重点实验室, 昆明 650201; 2 中国科学院大学, 北京 100049;
3 世界农用林业中心东亚和中亚区域办公室, 昆明 650201; 4 *Biomaterial Science*, *Graduate School of Agriculture*,
Kyoto University, *Kitashirakawa Oiwake*, Kyoto Prefecture, Japan; 5 *Department of Plant Sciences*, *Faculty of Agriculture*,
Rajarata University of Sri Lanka, Anuradhapura, Sri Lanka; 6 *Wildlife Conservation Society*, Yangon, Myanmar;
7 *Cibodas Botanic Garden*, *Indonesian Institute of Sciences*, Cianjur, West Java, Indonesia)

摘要: 利用地面观测和单绳上树法初次对布龙自然保护区勐宋片区开展的附生维管植物调查表明: 1) 在6个样地77株宿主上 (共调查96株乔木, 占地约0.2 ha), 共有1 756株、丛个体, 隶属14科47属103种; 相比世界其他区域, 物种丰富度处于旧世界热带水平区间, 高于温带, 但明显低于新世界热带水平; 2) 兰科植物为最丰富的类群 (60%), 其次为蕨类植物 (24%), 其他类群占16%; 3) 垂直分布特征研究表明, 距地面10~15 m的中等高度带为物种最丰富的区间, 约有51%的物种; 0~5 m高度带为个体数量最多的区间, 共有约24%个体, 揭示了除中等高度带以外的另一个重要附生生境; 4) 常见的绞杀型榕属植物未见, 而半附生植物密脉鹅掌柴 (*Schefflera elliptica*) 和多蕊木 (*Tupidanthus calyptratus*) 数量较多。

关键词: 附生维管植物; 垂直分布; 生物多样性; 布龙自然保护区; 西双版纳; 中国
中图分类号: Q 948 **文献标志码**: A **文章编号**: 2095-0845(2015)03-327-12

Diversity and Vertical Distribution Characteristics of Vascular Epiphytes in Bulong Nature Reserve Mengsong Section, Xishuangbanna

ZHAO Ming-xu[1,2,3], Geekiyanage Nalaka[4,5], Harrison Rhett Daniel[1,3]**, XU Jian-chu[1,3], Khin Myo Myo[6], Ridwan Nurdiana Dian[7], Paudel Ekananda[1,2,3]

(1 *Key Laboratory for Plant Diversity and Biogeography of East Asia*, *Kunming Institute of Botany*, *Chinese Academy of Sciences*,
Kunming, Yunnan 650201, China; 2 *University of Chinese Academy of Sciences*, Beijing 100049, China; 3 *World Agroforestry Centre*,
East and Central Asia, Kunming, Yunnan 650201, China; 4 *Biomaterial Science*, *Graduate School of Agriculture*, *Kyoto University*,
Kitashirakawa Oiwake, Kyoto Prefecture, Japan; 5 *Department of Plant Sciences*, *Faculty of Agriculture*, *Rajarata*
University of Sri Lanka, Anuradhapura, Sri Lanka; 6 *Wildlife Conservation Society*, Yangon, Myanmar;
7 *Cibodas Botanic Garden*, *Indonesian Institute of Sciences*, Cianjur, West Java, Indonesia)

Abstract: The first survey of vascular epiphytes was conducted using ground based inventory assisted by single rope technique in the recently-established Bulong Nature Reserve, Xishuangbanna, China. Results indicated that vascular epiphytes were abundant and diverse there. On a total of 77 phorophytes in six plots (96 trees were examined in to-

---

* Funding: National Key Basic Research Program of China (2014CB954100); The Applied Fundamental Research Foundation of Yunnan Province (2014GA003)

** Author for correspondence; E-mail: r.harrison@cgiar.org

Received date: 2014-08-13, Accepted date: 2014-10-28

作者简介: 赵明旭 (1984-) 男, 博士, 从事植物分类学和附生植物群落生态学研究。E-mail: zhaomingxu.sfa.kmy@gmail.com

tal, covered *ca.* 0.2 ha area), 1 756 individuals were recorded and were identified to 103 species (47 genera, 14 families). Compared with other regions, the epiphytes were as diverse as Paleotropics, and more diverse than temperate zone, but significantly less than the Neotropics. Orchids and ferns comprised 60%, 24% of the total flora, respectively, while others only took up 16%. The highest species richness and richest life-form diversity was found in the middle canopy zone from 10 to 15 m (51% of total species), where also supported high individual abundance (19% of total individuals). Besides the middle canopy, the most abundant zone of epiphyte individuals was detected at the base of the trunk (zone 0-5 m, 24% of total individuals and 37% of total species), indicating another important niche for epiphytes in this forest environment. Primary hemiepiphytic figs were rare in the area and were not found on the surveyed host trees, while hemiepiphytic Araliaceae species (*Schefflera elliptica* and *Tupidanthus calyptratus*) were popular.

Key words: Vascular epiphyte; Vertical distribution; Biodiversity; Bulong Nature Reserve; Xishuangbanna; China

A high diversity of epiphytes is one of the generally-recognized and distinct characteristics of tropical rain forests. Epiphytes make up 25% or more of the vascular plant diversity in certain Central Amazonian forests (Küper *et al.*, 2004), and a study in Venezuela found that over 50% of all vascular plant species were epiphytes (Kelly *et al.*, 1994). However, when extra-tropical regions are included, a large number of studies confirmed that, globally, about 8%-10% of vascular plants are epiphytes (Gentry and Dodson, 1987; Benzing, 1990; Lowman and Rinker, 2004; Zotz, 2013).

Most studies on epiphyte have been conducted in the Neotropics and tropical Africa (Hsu and Wolf, 2009; Table 3). Relatively few surveys of epiphyte diversity have been made in tropical Asia, especially in China, although some exist for subtropical China (Wang *et al.*, 1996; Xu and Liu, 2005; Yang, 2008). The diversity of epiphyte community in Hainan Island was recently investigated, and found to be much lower than in the Neotropics, but other aspects of epiphyte ecology, such as their vertical stratification, appeared similar (Liu, 2010; Liu *et al.*, 2010).

Xishuangbanna comprises the largest area of tropical forest in China (Zhu, 2006) and forms part of the Indo-Burma biodiversity hotspot (Myers *et al.*, 2000). More than 4 000 species of seed plant occur in the area (19 690 km^2, Zhu and Yan, 2012). Although Wang and Zhu suggested that vascular epiphytes were a prominent characteristic of tropical montane rainforest in Xishuangbanna (Wang *et al.*, 2001; Zhu, 2006), quantitative surveys of epiphyte diversity and vertical distribution characteristics have not been conducted.

The vertical gradient is a defining feature of forests, because habitat structure and microclimate factors (light, water, and mineral nutrition) (Benzing, 1990, 2012) are vertically organized (Dhanmanonda, 1996; Steege and Cornelissen, 1989; Benzing, 1990; McCune *et al.*, 1997; Lowman and Rinker, 2004). With increasing height, the humidity, light availability, and substrate conditions (including pH) all vary-which defines different microhabitats for epiphyte communities (Pittendrigh, 1948; Johansson, 1974; Kelly, 1985; Cornelissen and Steege, 1989; Parker, 1995; Dhanmanonda, 1996; Freiberg, 1997; Krömer *et al.*, 2007). For example, Dhanmanonda (1996) found that light availability increased exponentially with increasing height above the forest floor, and epiphytes vertical distribution characteristics had been shown to be influenced by the photon flux density (Pittendrigh, 1948; Steege and Cornelissen, 1989). Humidity is also believed to be one of the most important factors in determining epiphyte community assembly (Steege and Cornelissen, 1989; Pittendrigh, 1948; Freiberg, 1997; Nieder *et al.*, 1999). The adaptation of epiphytes, in terms of their anatomy and physiology, to vertical microhabitat heterogeneity, has been comprehensively reviewed by Benzing (1990).

Our aims in this research are to describe the diversity and vertical distribution characteristics of epiphyte community in the tropical montane forest of Xishuangbanna, addressing this knowledge gap in tropical China. Thus, our study is an observational study aimed at documenting diversity, and, hence, can only be suggestive of the community assembly processes (Johansson, 1974; Kelly, 1985; Zotz, 2007).

1 Methods

1.1 Study site

Our study was conducted in the recently-established Bulong Nature Reserve, Mengsong Section (MS-BNR, 2009), in Xishuangbanna, China (Fig. 1). The vegetation type has been categorized as tropical montane rainforest and monsoon evergreen broadleaf forest, the former located in relatively humid regions (montane valley, riparian), while the latter usually is found on the dry slopes. The elevation ranges from 1 110 m to 2 039 m (the peak of Sanduogeque), and mean monthly temperatures fluctuates between 15–21 ℃ (at 1 600 m asl). The study site has a typical monsoon climate (greatly influenced by the India Ocean monsoons) and the annual precipitation ranges between 1 800–2 379 mm, 80% of which occurs between the months of May and October. The atmosphere has an annual relative humidity of 83% (Zhu *et al.*, 2004).

1.2 Field observations

Field work was conducted during the dry season November to December, 2012, when the crown layers were clear and epiphytes were easy to observe. Six previously-established, one hectare (100 m × 100 m), permanent sampling plots in the old growth area of the forest (*ca.* 35 m of canopy height) in MS-BNR were selected for this present study, three of which were located in a tropical montane rainforest and three in an evergreen broadleaf forest (Fig. 1, Table 1). Plots were separated by a minimum straight

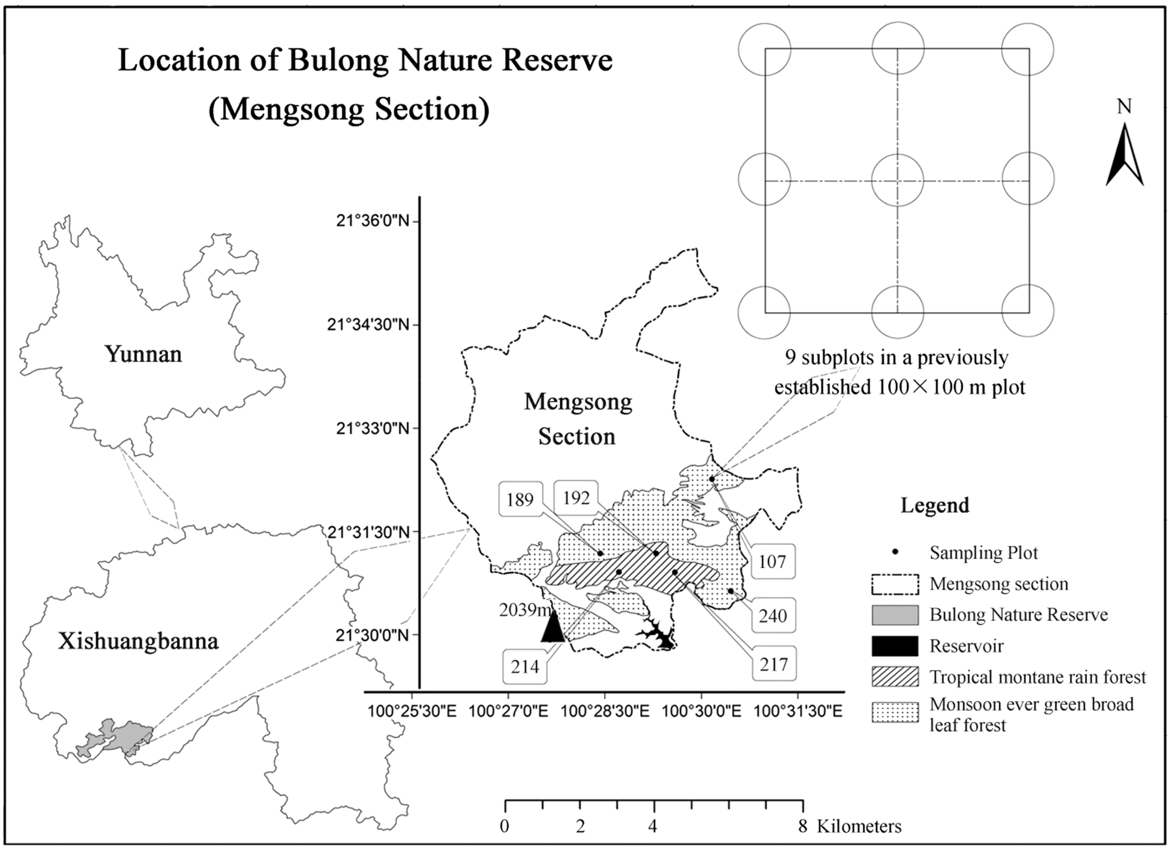

Fig. 1 Location of sampling plots and the MS-BNR, Xishuangbanna. The map showing the old growth forest area of MS-BNR, the remaining blank areas are mainly covered by secondary forest or open land

Table 1 Basic information of sampling plots in MS-BNR, Xishuangbanna

Plot	Elevation /m	Forest type	Dominate tree	Host occupancy /%	Basal area /Plot area(m^2/ha)	Epiphyte No. of Ind. /No. of species
107	1450	MEBF	CASMEK, STYTON	56.3	24.4	217/24
189	1700	MEBF	CASMEK, LITMAR	87.5	22.2	264/31
192	1785	MEBF	CASMEK, ANNFRA	100.0	25.6	389/30
214	1670	TMRF	SYZBRA, LITBAC	81.3	45.6	399/48
217	1700	TMRF	ALAKUR, CRYBRA	93.8	22.2	310/36
240	1750	TMRF	CALPOL, CASCAL	62.5	34.1	177/21

Note: MEBF = Monsoon Evergreen Broadleaf Forest, TMRF = Tropical Montane Rain Forest. Dominate trees were selected by the first two importance value in a plot (nine sub plots tree data was applied, respectively). CASMEK = *Castanopsis mekongensis*, STYTON = *Styrax tonkinensis*, LITMAR = *Litsea martabanica*, ANNFRA = *Anneslea fragrans*, SYZBRA = *Syzygium brachythyrsum*, LITBAC = *Lithocarpus bacgiangensis*, ALAKUR = *Alangium kurzii*, CRYBRA = *Cryptocarya brachythyrsa*, CALPOL = *Calophyllum polyanthum*, CASCAL = *Castanopsis calathiformis*. Host occupancy was calculated by 100 × epiphyte occupied trees/total trees (16) in a plot

line distance of 700 m and a maximum of 3 600 m. Nine 10 m-radius circle subplots were set inside a big plot, and trees (dbh ≥ 10 cm, dbh = diameter at breast height) were measured and identified. At each big plot, a random point was marked near the central subplot of nine, and the 16 nearest trees (dbh ≥ 10 cm, covering an area of approximately 10 m radius subplot) were examined for epiphytes, and 96 trees were checked in total.

Binoculars and a spotting-scope were first used to check host tree roughly, only if epiphyte was detected on the ground, we would access the crown using single rope technique at least to the main fork site to assist specimen collecting and the latter epiphytes counting, attaching height measurement work (Perry, 1978). A telescopic pruning shears with maximum 5 m was also implemented to assist the collecting process. Digital photographs were also taken to document observations and assist in the identification process. Due to identification barriers, all small seedlings were omitted and orchids that were hard to identified without flower were all kept alive in greenhouses until identified, then herbarium specimen were made.

Epiphyte attaching height above ground was measured using a 5 m pole, or, for those species distributed in the outer of crown, where could not be accessed, by estimating the height using the 5 m pole as a reference. When estimating heights, the observer stood at least 20 m away from the tree. Epiphytes that covered a substantial portion of the host crown (creeping or clustered species, like *Pyrrosia lingua* and *Cylindrolobus marginatus*), the height was taken from the lowest to the highest points.

Two schemes of forest canopy zonation were applied in the former studies, six vertical tree zones (Steege and Cornelissen, 1989) and equal height interval vertical tree zones (Zotz and Schultz, 2008), both were proved to be efficient approaches, we followed the latter and forest canopy was divided into seven height zones using a 5 m interval (the highest crown layer was about 35 m) as several other studies did (Zotz and Schultz, 2008; Liu *et al.*, 2010), hence our results could be compared both in the tropical forest domestically and abroad, and the micro environmental factors were more consistent in the parallel upper zones than the former arc-shaped scheme.

To define epiphyte individuals, we referred to the individual definition of ‘stand’ (Sanford, 1968). A stand was defined as a cluster of pseudobulbs (or the same epiphyte species leaves) was spatially separated from another—either by an area devoid of epiphytes or occupied by other species. When the same area was occupied by an intermingling of more than one species, one stand was counted for each species present. If a stand of epiphyte covered two or more vertical zones, especially those with long rhizomes or large-area clustered pseudobulbs, both individual number and its name were repetitively recorded in each zone. Epiphyte species were registered either by scientific or morphological names in the field table, and the individual number of each species was also recorded. Specimens were identified by comparing to species at the herbarium at the Xishuangbanna Tropical Botanical Garden. Vouchers were lodged at the Kunming Institute of Botany. The plant names and families followed *Flora of China* (eFloras, 2008).

The epiphyte life forms were defined following Benzing (1990) scheme I, and categories were based on relationships to the host (A. Autotrophs): true epiphyte, hemiepiphyte, facultative and accidental epiphyte. However, when we applied these rules in field, distinguishing of epiphytic life forms was difficult in some cases for the lack of former quantitative information. Here, besides the definition in the scheme, some additional rules were set: we grouped the species can live on trees, rocks or any surfaces where the substrate layers was thin or absent (for example, the moss mat or the thin layer of canopy soil) into true epiphyte, like most of the epiphytic orchids and ferns. Hemiepiphyte referred to those species both had epiphytic and terrestrial phases in their whole life processes, and according to first living on tree or ground, they could be divided into primary and secondary hemiepiphyte sub-categories. To avoid any confusion of lianas and secondary epiphyte (Zotz, 2013), we excluded the secondary epiphyte from hemiepiphyte category, such as Aroids, Piperoids and climber *Ficus* spp., only species like epiphytic *Schefflera* spp. would root in ground finally, were retained as primary hemiepiphyte. Facultative epiphyte refers to species could inhabit forest canopies and the ground interchangeably, such as *Peperomia* spp., *Medinilla* spp. and *Hedychium* spp. Those species only few individuals anchored in the canopy occasionally, but most of their individuals of rooting in the ground, were assigned to accidental epiphyte category. The species records from *Flora of China* and *Flora of Yunnan* (Wu, 2006) were consulted during the life from determination.

2 Results

2.1 Floristics

Across the six plots, 96 trees were surveyed. Nineteen trees were without any epiphytes, and the remaining 77 trees (80%) were colonized by 1 756 epiphyte individuals, which were identified to 103 species in 46 genera, 14 families. The epiphyte community in MS-BNR was dominated by Orchidaceae (60%) and ferns (24%), while other epiphytic species only took up 16% of the total flora recorded (Fig. 2, Appendix I).

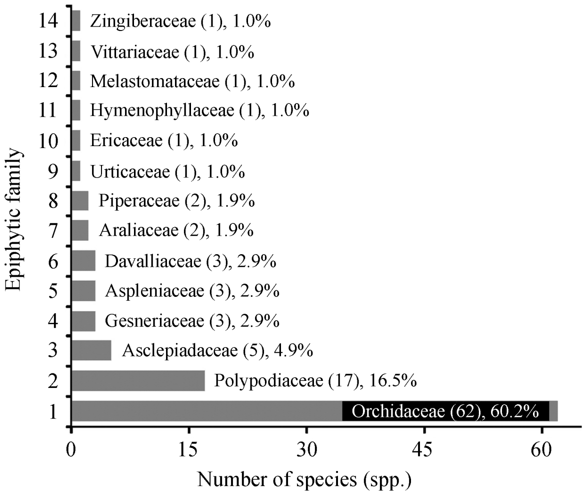

Fig. 2　Epiphyte community floristic composition of MS-BNR, Xishuangbanna

2.2 Life form composition

Ninety-Six species of true epiphytes were recorded. All 62 orchid species and all 25 ferns belonged to this group. The most common species were *Mycaranthes pannea* (215 individuals) and *Davallia trichomanoides* (171 individuals). Other true epiphytes included five Asclepiadaceae, three Gesneriaceae, and one Ericaceae species. Surprisingly, we did not observe any strangler figs in this tropical area, which are normally a prominent characteristic of tropical rain forests (Harrison *et al.*, 2003). *Tupidanthus calyptratus* and *Schefflera elliptica* were the hemiepiphytes we recorded. Five epiphytes were facultative in character, occurring as both terrestrial and epiphytic plants and no accidental epiphyte were found.

2.3 Species and life forms vertical distribution

A summary of the vertical profile of epiphytes observed in MS-BNR is given in Table 2 and Fig. 3. The highest species richness was found in 10–15 m zone, which was in the mid-canopy of the forest, and the lowest zone was >30 m tree height zone, on the topmost canopy layer. However, in terms of the abundance of individuals, the base of host trees was the most important niche, where about 24% of epiphyte individuals were found. The highest attached species, *Hoya chinghungensis*, was observed at a height of 32 m.

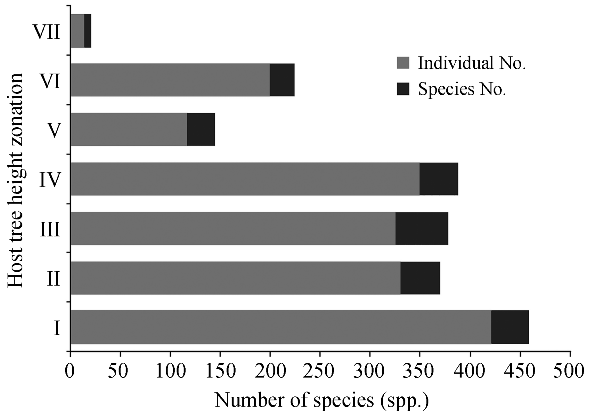

Fig. 3 Vertical distribution profile of epiphyte community of MS-BNR, Xishuangbanna

As to the vertical profile of life-forms, true epiphytes dominated in terms of abundance in each height zone, and above 20 m of tree height, the proportion approached 100%. In the 15–20 m zone and the 25–30 m zone, *Hedychium villosum* and *Micholitzia obcordata* were the only facultative epiphytes sharing the upper canopy with true epiphytes. True epiphytes showed a humped shape of distribution of species richness along the vertical zones, while facultative epiphytes declined in species richness with increasing height. The hemiepiphytes were abundant in the mid-zones, but only limited around the main fork area.

2.4 Vertical zone details of the epiphyte community

0–5 m zone: Usually, this is a moist area with thick mosses, very similar to the habitat of moss covered rocks or hard soil surfaces, and is a transitional zone for terrestrial to epiphytic lives. It is typified by sufficient water and mineral nutrients supply, but light availability is usually low. Overall, we observed 421 epiphyte individuals from 38 species in 11 families in this zone. About 60.5% of these epiphytes were ferns (23 spp.), mainly Polypodiaceae species (15 spp.), and the most abundant species were *Pyrrosia lingua* and *Lepisorus scolopendrium*. Other prominent epiphytes in this zone were Orchidaceae species (eight spp.). Most of the orchids growing here were species that were generalist (widely distributed throughout the vertical zones), like *Pholidota articulata*, *Dendrobium falconeri* and *Dendrobium chrysotoxum*. However, *Liparis cespitosa* and *Dendrobium compactum* were specialists (limited distribution species) in this zone. The remaining epiphytes found in this zone included species of Aspleniaceae, Davalliaceae, Hymenophyllaceae and so on. Excluding true epiphytes (33 spp.), facultative epiphyte was the most abundant life-form. Most of these facultative epiphytes had succulent functional organs to survive in dry season, such as leaves, stems, and roots (for instance, the stem and leaves of *Peperomia blanda*, *Pellionia heteroloba* and *Medinilla himalayana*, and

Table 2 Occurrence of vascular epiphytes in the vertical profile of the MS-BNR forest

Height/m	Indi. No.	Spp. No.	Indi. (% total)	Spp. (% total)	Typical species (>10% of total height zone)
0–5	421	38	24	37	*Haplopteris flexuosa*, *Davallia trichomanoides*
5.1–10	330	40	19	39	*Davallia trichomanoides*
10.1–15	325	53	19	51	*Mycaranthes pannea*
15.1–20	349	39	20	38	*Mycaranthes pannea*, *Coelogyne viscosa*, *Coelogyne fuscescens*
20.1–25	117	28	7	27	*Bulbophyllum levinei*, *Mycaranthes pannea*
25.1–30	200	25	11	24	*Mycaranthes pannea*, *Cylindrolobus marginatus*
>30.1	14	7	1	7	*Mycaranthes pannea*, *Bulbophyllum pectinatum*

Pseudostems of *Hedychium villosum*).

5−10 m zone: This height zone forms the transition from the trunk to the main fork. Compared to the lower part of the tree trunk, because most of the stem flow, this region is drier than-but still not as dry as-the upper layers of crown. 40 species in 10 families of 330 individuals were recorded in this zone. The flora composition of the epiphyte community in zone 5−10 m was similar to that in zone 0−5 m, but orchids (17 spp.) became more abundant, and the most common species were *Coelogyne viscosa* and *Dendrobium falconeri*. Ferns were also a prominent part of the epiphyte community in this zone (18 spp.), still mainly Polypodiaceae species (11 spp.). The most abundant ferns were *Davallia trichomanoides* and *Polypodiastrum argutum*. Hemiepiphyte (*Schefflera elliptica*) made an appearance here, and the remaining nine species belonged to Aspleniaceae, Davalliaceae Hymenophyllaceae, Vittariaceae, Gesneriaceae, Araliaceae, Piperaceae and Urticaceae.

10−15 m zone: The micro habitat environmental factors here are all at a moderate level, together with sufficient surfaces for adhering, the epiphyte community diversity was expected high in this zone. To that end, just as we anticipated, epiphyte species diversity was highest in this zone, with 53 species in nine families and 325 individuals represented. The dominant species were *Mycaranthes pannea* and *Davallia trichomanoides*. Orchids (36 spp.) took up the most proportion of the community. Ferns were also a substantial component (11 spp.), and again were mainly Polypodiaceae species (7 spp.), like *Pyrrosia lingua*, *Lepisorus henryi*, and *Lepisorus sinensis*. Other ferns included *Asplenium antrophyoides*, *Humata griffithiana*, and *Haplopteris flexuosa*. Another characteristic of this zone was the prevalence of hemiepiphytes *Schefflera elliptica* and *Tupidanthus calyptratus*, the two hemiepiphytes were both found in this zone. The remaining epiphytes of this zone included Asclepiadaceae, Piperaceae, Gesneriaceae and Davalliaceae species, such as *Dischidia tonkinensis*, *Peperomia blanda*, and *Aeschynanthus austroyunnanensis*.

15−20 m zone: The microhabitat in this zone becomes drier, and branches have smoother bark and relatively-smaller adherence surfaces, but light conditions improve. A total of 349 individuals among 39 species in seven families were recorded. Dominant species here were *Mycaranthes pannea* and *Coelogyne viscosa*. Orchids still comprised the majority of species (23 spp.), followed by ferns (10 spp.). Species like *Coelogyne fuscescens*, *Polypodiastrum argutum*, and *Pholidota yunnanensis* were all prevalent in this zone. The six remaining species were from Asclepiadaceae, Gesneriaceae and Zingiberaceae. Epiphyte life forms diversity decreased in this zone, besides the true epiphytes, only one facultative species (*Hedychium villosum*) were recorded.

20−25 m zone: We recorded 117 individuals among 28 species in five families in this zone. Compared to the typical densely clustered appearances of epiphyte community observed in lower zones, epiphytes here were scattered throughout on smaller branches and forks. The dominant epiphytes were orchids, *Bulbophyllum levinei* and *Mycaranthes pannea*, and the proportion of orchids in the community was high (20 spp. or 71%), while there were fewer ferns (6 spp. or 21%), including *Pyrrosia lingua*, *Araiostegia perdurans* and *Lepisorus scolopendrium*. *Agapetes mannii* here was the only Ericaceae epiphytic species in the study area.

25−30 m zone: Most epiphytes in this zone were distributed on the relatively-larger branches, only very few species occurred on the smaller forks or twigs inside the canopy. 25 species, 200 individuals in four families were observed here, and the community was dominated by *Mycaranthes pannea* and *Cylindrolobus marginatus*. Most species were orchids (19 spp.), and four Polypodiaceae, one Asclepiadacea, and one Ericaceae species constituting the remaining community members.

30−35 m zone: This zone covers the uppermost layer of canopy, and was the most instable of habitat among all zones, and could be described as the harshest environment for most epiphytes. Only 14 individuals of seven species in four families occurred here. Most of these species were generalists occurring throughout the vertical profile, including orchids (four spp.) like *Mycaranthes pannea* and *Bulbophyllum pectinatum*, and ferns (two spp.), *Davallia trichomanoides* and *Pyrrosia lingua*. *Hoya chinghungensis* (Asclepiadaceae) six individuals were only found in upper zones (16-32 m of canopy) and seemed to be a specialist to high canopy layers. *Dendrolirium tomentosum* was also only found in this zone; however, as only one individual was observed, we cannot deduce anything about the vertical niche of this species.

3 Discussion

3.1 Floristics

This is the first study to document the vascular epiphyte community in MS-BNR, and the first such study performed in Xishuangbanna, which is otherwise well-known for its high plant diversity (Zhu and Yan, 2012). Although it was still an incomplete inventory of the area, we recorded 103 species in 47 genera and 14 families on 77 host trees (total plot area *ca*. 0.2 ha), confirming the assertion that epiphytes are abundant and diverse in the tropical area (Küper *et al*., 2004).

The survey of epiphytes in Huanglian mountain cloud forest found 151 species (including lianas like Piperoids, Aroids and Vitis) on 233 trees (Yang, 2008). Liu (2010) found 120 species in Bawang Ridge in Hainan Island among six forest types over a 3.6 ha area. Other studies from China reported from subtropical or warm temperate areas all recorded lower levels of species richness than we found at MS-BNR. For example, Xu and Liu (2005) only found 32 species on 80 host trees in a montane moist evergreen broad-leaved forest on Ailao Mountain (about 200 km north of MS-BNR), and in a semi-humid evergreen broad-leaved forest only nine species of epiphyte were found in 0.1 ha area (Xu *et al*., 2006). Similarly, Liu *et al*. (2010) found 27 species in a 0.6 ha natural tropical coniferous forest, while Wang *et al*. (1996) found 41 species of obligate vascular epiphytes in a subtropical evergreen broadleaf forest. Hsu (2009) recorded a high level of epiphyte species richness for the whole of Taiwan (336 species, including lianas like Figs, Piperoids and Aroids), not only that was based on the total flora for a large island in many ecological zones, but also included the confusing secondary hemiepiphytes (Hsu and Wolf, 2009).

Epiphyte research in tropical Africa suggests epiphyte species richness is similar to the levels we found in MS-BNR and for tropical China in general, much higher than the Temperate zone (Hsu and Wolf, 2009, Table 2), but much lower than the Neotropics. This may be explained by the lack some important epiphyte families like Bromeliaceae (*ca*. 1 770 epiphytic spp.), Cactaceae (*ca*. 125 epiphytic spp.) and some Orchid genera like *Pleurothallis* (1 500 spp.) in the Paleotropics (Zotz, 2013).

3.2 Vertical structure

Different micro-environmental factors are thought to structure the vertical distribution of epiphytes, as described in several studies (Johansson, 1974; Steege and Cornelissen, 1989; Benzing, 1990; Lowman and Rinker, 2004; Zotz, 2007; Krömer *et al*., 2007). Moreover, investigations into microclimatic variation have confirmed the expected patterns of vertical heterogeneity (Dhanmanonda, 1996; Freiberg, 1997). We found that the middle canopy had the highest species richness, which is consistent with earlier studies (Steege and Cornelissen, 1989; Freiberg, 1996; Zotz and Schultz, 2008; Pos and Sleegers, 2010). The humped shape distribution profile throughout the forest canopy may be explained by the moderate water and light conditions in the middle canopy, combined with the relative larger effective surface area and more suitable substrate (Nadkarni, 1984; Freiberg and Freiberg, 2000). Krömer *et al*. (2007) found that, besides the diverse and abundant epiphyte flora of the middle canopy, there was a conspicuous epiphyte flora in the understory (40% aroids, 35%-40% piperoids and 25%-30% ferns).

We did not check the epiphyte flora on smaller trees (dbh< 10 cm), but obtained a similar result, that the highest abundance of epiphyte individuals was observed in 0−5 m zone.

True epiphytes are the overwhelming majority in every zone, and they mix with little proportion with other epiphytic life-forms in and under middle zones. Facultative and hemiepiphytes could be hardly found above 15 m of canopy. The tree base area, corresponding to 0−5 m zone, is a transition area from terrestrial to epiphytic lives. Much of the host tree base area is covered by a thick moss mat in humid environments (Freiberg, 1997), which could be a good explanation of abundant facultative epiphytes here. In 5−10 m and 10−15 m zones, the appearance and prevailing of hemiepiphytes was the most apparent characteristic. The upper zones of canopy (15−35 m), where almost only true epiphytes were found, had more than half of the true epiphytes comprised of orchids. Epiphytic orchids are generally regarded as drought-enduring plants, and have succulent structures (pseudobulb, terete leaf, or fleshy root) (Benzing, 1990), thus can be used as a good explanation for this phenomenon.

4 Conclusion

Our survey recorded a high diversity of epiphytes, as is generally reported in studies of tropical forests, and confirmed a similar humped vertical structuring of the epiphyte community around mid canopy. The MS-BNR could potentially provide a protected habitat for a large diversity of epiphytes. We suggest future studies focus on species of conservation concern, as many other forests in China-and even in Xishuangbanna-have been over-harvested for epiphytes (in particular, orchids, such as medicinal and ornamental *Dendrobium* spp., *Vanda* spp. and *Cymbidium* spp.).

Acknowledgement: We thank Xishuangbanna Tropical Botanical Garden and the Program for Field Studies in Tropical Asia for supporting the "Advanced Field Course in Ecology and Conservation" in Xishuangbanna (AFEC-X) during which the field research for this study took place. We wish to thank the resource staff and colleagues on the AFEC-X 2012 for critical comments and suggestions. Funding for ZM and KMM was provided by the Centre for Mountain Ecosystem Studies. Other authors were funded by AFEC-X.

References:

Benzing DH, 1990. *Vascular Epiphytes: General Biology and Related biota* [M]. UK: Cambridge University Press

Benzing, DH, 2012. *Air Plants: Epiphytes and Aerial Gardens* [M]. Ithaca: Cornell University Press

Cornelissen Jt, Steege HT, 1989. Distribution and ecology of epiphytic bryophytes and lichens in dry evergreen forest of Guyana [J]. *Journal of Tropical Ecology*, **5** (2): 131—150

eFloras, 2008. Published on the Internet [OL]. http://www.efloras.org [accessed 2012-2014] Missouri Botanical Garden, St. Louis, MO & Harvard University Herbaria, Cambridge, MA.

Dhanmanonda P, 1996. Three-dimensional distribution of light intensity in the dry dipterocarp forest at Sakaerat, Northeastern Thailand [J]. *Thai Journal of Forestry*, **15** (2): 81—88

Freiberg M, 1996. Spatial distribution of vascular epiphytes on three emergent canopy trees in French Guiana [J]. *Biotropica*, **28** (3): 345—355

Freiberg M, 1997. Spatial and temporal pattern of temperature and humidity of a tropical premontane rain forest tree in Costa Rica [J]. *Selbyana*, **18** (1): 77—84

Freiberg M, Freiberg E, 2000. Epiphyte diversity and biomass in the canopy of lowland and montane forests in Ecuador [J]. *Journal of Tropical Ecology*, **16** (05): 673—688

Gentry AH, Dodson C, 1987. Diversity and biogeography of neotropical vascular epiphytes [J]. *Annals of the Missouri Botanical Garden*, **74** (2): 205—233

Harrison RD, Hamid AA, Kenta T *et al.*, 2003. The diversity of hemi-epiphytic figs (Ficus; Moraceae) in a Bornean lowland rain forest [J]. *Biological Journal of the Linnean Society*, **78** (4): 439—455

Hsu R, Wolf JH, 2009. Diversity and phytogeography of vascular epiphytes in a tropical-subtropical transition island, Taiwan [J]. *Flora*, **204** (8): 612—627

Johansson D, 1974. Ecology of vascular epiphytes in West African rain forest [J]. *Acta Phytogeographica Suecica*, **59**: 1—136

Kelly D, Tanner E, Lughadha *et al.*, 1994. Floristics and biogeography of a rain forest in the Venezuelan Andes [J]. *Journal of Biogeography*, **21** (4): 421—440

Kelly DL, 1985. Epiphytes and climbers of a Jamaican rain forest: vertical distribution, life forms and life histories [J]. *Journal of Biogeography*, **12** (3): 223—241

Kelly DL, O'Donovan G, Feehan J *et al.*, 2004. The epiphyte communities of a montane rain forest in the Andes of Venezuela: patterns in the distribution of the flora [J]. *Journal of Tropical Ecology*, **20** (6): 643—666

Krömer T, Kessler M, Gradstein SR, 2007. Vertical stratification of vascular epiphytes in submontane and montane forest of the Bolivian Andes: the importance of the understory [J]. *Plant Ecology*, **189** (2): 261—278

Küper W, Kreft H, Nieder J *et al.*, 2004. Large-scale diversity patterns of vascular epiphytes in Neotropical montane rain forests [J]. *Journal of Biogeography*, **31** (9): 1477—1487

Liu G, 2010. Diversity and distribution of vascular epiphytes of tropical forests in Hainan Island, China [D]. Dissertation, Chinese academy of forestry, Beijing

Liu G, Ding Y, Zang R *et al.*, 2010. Diversity and distribution of vascular epiphytes in the tropical natural coniferous forest of Hainan Island, China [J]. *Chinese Journal Plant Ecology*, **34** (11): 1283—1293

Lowman MD, Rinker HB, 2004. *Forest Canopies* [M]. Sandiego, California, USA: Academic Press, 2004

McCune B, Amsberry K, Camacho F *et al.*, 1997. Vertical profile of epiphytes in a Pacific Northwest old-growth forest [J]. *Northwest Science*, **71** (2): 145—152

Myers N, Mittermeier RA, Mittermeier CG *et al.*, 2000. Biodiversity hotspots for conservation priorities [J]. *Nature*, **403** (6772): 853—858

Nadkarni NM, 1984. Epiphyte biomass and nutrient capital of a neotropical elfin forest [J]. *Biotropica*, **16** (4): 249—256

Nieder J, Engwald S, Barthlott W, 1999. Patterns of neotropical epiphyte diversity [J]. *Selbyana*, **20** (1): 66—75

Parker GG, 1995. Structure and microclimate of forest canopies [A] // Lowman MD, Nadkarni NM ed., *Forest Canopies* [M], 1st edn. San Diego, USA: Academic Press, 73—106

Perry DR, 1978. A method of access into the crowns of emergent and canopy trees [J]. *Biotropica*, **10**: 155—157

Pittendrigh CS, 1948. The bromeliad-Anopheles-malaria complex in Trinidad. I-The bromeliad flora [J]. *Evolution*, **2** (1): 58—89

Pos ET, Sleegers ADM, 2010. Vertical distribution and ecology of vascular epiphytes in a lowland tropical rain forest of Brazil [J]. *Boletim do Museu Paraense Emílio Goeldi Bol Mus Para Emilio Goeldi Ciências Naturais*, **5** (3): 335—344

Sanford WW, 1968. Distribution of epiphytic orchids in semi-deciduous tropical forest in southern Nigeria [J]. *The Journal of Ecology*, **56** (3): 697—705

Steege Ht, Cornelissen J, 1989. Distribution and ecology of vascular epiphytes in lowland rain forest of Guyana [J]. *Biotropica*, **21** (4): 331—339

Wang J, Wei P, Huang Z, 1996. The epiphyte of Dinghu Mountain [J]. *Journal of Jilin Agricultural University*, **18** (3): 40—44

Wang H, Zhu H, Li B, 2001. A study on the tropical montane rain forest in Mengsong, Xishuangbanna, S. Yunnan [J]. *Guihaia*, **21** (4): 303—314

Wu ZY, 2006. *Flora of Yunnan* [M]. Beijing: Science Press

Xu H, Liu W, 2005. Species diversity and distribution of epiphytes in the montane moist evergreen broad-leaved forest in Ailao Mountain, Yunnan [J]. *Biodiversity Science*, **13** (2): 137—147

Xu H, Liu W, Shen Y *et al.*, 2006. A preliminary study of epiphytes in semi-humid evergreen broad-leaved forest in Stone-forest Karst Region, Yunnan Province [J]. *Guihaia*, **26** (1): 43—48

Yang J, 2008. Biodiversity and spatial distribution of vascular epiphytes in cloud forest on Huanglian Mountain, Yunnan Province [D], MSc Thesis, Kunming Institute of Botany, Chinese Academy of Sciences, Beijing

Zhu H, Wang H, Li B, 2004. Plant diversity and physiognomy of a tropical montane rain forest in Mengsong, South Yunnan, China [J]. *Acta Phytoecologica Sinica*, **28** (3): 351—360

Zhu H, 2006. Forest vegetation of Xishuangbanna, south China [J]. *Forestry Studies in China*, **8** (2): 1—58

Zhu H, Yan L, 2012. *Native Seed Plants in Xishuangbanna of Yunnan* [M]. Beijing: Science Press

Zotz G, 2007. Johansson revisited: the spatial structure of epiphyte assemblages [J]. *Journal of Vegetation Science*, **18** (1): 123—130

Zotz G, Schultz S, 2008. The vascular epiphytes of a lowland forest in Panama—species composition and spatial structure [J]. *Plant Ecology*, **195** (1): 131—141

Zotz G, 2013. The systematic distribution of vascular epiphytes—a critical update [J]. *Botanical Journal of the Linnean Society*, **171** (3): 453—481

Appendix I　The vascular epiphtes checklist of MS-BNR, Xishuangbanna

No.	Family/Speices	Habit
	Araliaceae	
1	*Schefflera elliptica* (Blume) Harms	PHE
2	*Tupidanthus calyptratus* J. D. Hooker & Thomson	PHE
	Asclepiadaceae	
3	*Dischidia tonkinensis* Costantin	TE
4	*Hoya chinghungensis* (Tsiang & P. T. Li) M. G. Gilbert & P. T. Li & W. D. Stevens	TE
5	*H. pandurata* Tsiang	TE
6	*H. villosa* Costantin	TE
7	*Micholitzia obcordata* N. E. Brown	TE
	Aspleniaceae	
8	*Asplenium antrophyoides* Christ	TE
9	*A. ensiforme* Wallich ex Hooker & Greville	TE
10	*A. yoshinagae* Makino	TE
	Davalliaceae	
11	*Araiostegia perdurans* (Christ) Copeland	TE
12	*Davallia trichomanoides* Blume	TE
13	*Humata griffithiana* (Hooker) C. Christensen	TE
	Ericaceae	
14	*Agapetes mannii* Hemsley	TE
	Gesneriaceae	
15	*Aeschynanthus andersonii* C. B. Clarke	TE
16	*A. austroyunnanensis* W. T. Wang	TE
17	*A. bracteatus* Wallich ex A. P. de Candolle	TE
	Hymenophyllaceae	
18	*Hymenophyllum polyanthos* (Swartz) Swartz	TE
	Melastomataceae	
19	*Medinilla himalayana* J. D. Hooker ex Triana	FE
	Orchidaceae	
20	*Acampe rigida* (Buchanan-Hamilton ex Smith) P. F. Hunt	TE
21	*Agrostophyllum callosum* H. G. Reichenbach	TE
22	*Ascocentrum ampullaceum* (Roxburgh) Schlechter	TE
23	*Bulbophyllum affine* Lindley	TE
24	*B. ambrosia* (Hance) Schlechter	TE
25	*B. corallinum* Tixier & Guillaumin	TE
26	*B. crassipes* J. D. Hooker	TE
27	*B. cylindraceum* Lindley	TE
28	*B. helenae* (Kuntze) J. J. Smith	TE
29	*B. levinei* Schlechter	TE
30	*B. nigrescens* Rolfe	TE
31	*B. odoratissimum* (Smith) Lindley	TE
32	*B. orientale* Seidenfaden	TE
33	*B. pectinatum* Finet	TE
34	*B. reptans* (Lindley) Lindley	TE
35	*B. shweliense* W. W. Smith	TE
36	*Callostylis rigida* Blume	TE
37	*Cleisostoma fuerstenbergianum* Kraenzlin	TE
38	*Coelogyne assamica* Linden & H. G. Reichenbach	TE
39	*C. fuscescens* Lindley	TE
40	*C. longipes* Lindley	TE
41	*C. ovalis* Lindley	TE
42	*C. prolifera* Lindley	TE
43	*C. schultesii* S. K. Jain & S. Das	TE
44	*C. viscosa* H. G. Reichenbach	TE
45	*Cylindrolobus marginatus* (Rolfe) S. C. Chen & J. J. Wood	TE
46	*Dendrobium brymerianum* H. G. Reichenbach	TE
47	*D. capillipes* H. G. Reichenbach	TE
48	*D. chrysanthum* Wallich ex Lindley	TE
49	*D. chrysotoxum* Lindley	TE
50	*D. compactum* Rolfe ex W. Hackett	TE

Appendix I continued

No.	Family/Speices	Habit
51	*D. cucullatum* R. Brown	TE
52	*D. falconeri* Hooker	TE
53	*D. fimbriatum* Hooker	TE
54	*D. harveyanum* H. G. Reichenbach	TE
55	*D. jenkinsii* Wallich ex Lindley	TE
56	*D. sinominutiflorum* S. C. Chen	TE
57	*D. spatella* H. G. Reichenbach	TE
58	*D. stuposum* Lindley	TE
59	*D. thyrsiflorum* H. G. Reichenbach ex André	TE
60	*D. wardianum* Warner	TE
61	*Dendrolirium tomentosum* (J. Koenig) S. C. Chen & J. J. Wood	TE
62	*Gastrochilus calceolaris* (Buchanan-Hamilton ex Smith) D. Don	TE
63	*Holcoglossum kimballianum* (H. G. Reichenbach) Garay	TE
64	*Liparis cespitosa* (Lamarck) Lindley	TE
65	*L. platyrachis* J. D. Hooker	TE
66	*L. viridiflora* (Blume) Lindley	TE
67	*Luisia magniflora* Z. H. Tsi & S. C. Chen	TE
68	*Mycaranthes pannea* (Lindley) S. C. Chen & J. J. Wood	TE
69	*Oberonia ensiformis* (Smith) Lindley	TE
70	*Otochilus albus* Lindley	TE
71	*O. fuscus* Lindley	TE
72	*O. porrectus* Lindley	TE
73	*Phalaenopsis deliciosa* H. G. Reichenbach	TE
74	*Pholidota articulata* Lindley	TE
75	*P. chinensis* Lindley	TE
76	*P. imbricata* Hooker	TE
77	*P. yunnanensis* Rolfe	TE
78	*Pinalia spicata* (D. Don) S. C. Chen & J. J. Wood	TE
79	*P. stricta* (Lindley) Kuntze	TE
80	*Robiquetia succisa* (Lindley) Seidenfaden & Garay	TE
81	*Vanda brunnea* H. G. Reichenbach	TE
	Piperaceae	
82	*Peperomia blanda* (Jacquin) Kunth	FE
83	*P. tetraphylla* (G. Forster) Hooker & Arnott	FE
	Polypodiaceae	
84	*Lemmaphyllum carnosum* (Wallich ex J. Smith) C. Presl	TE
85	*L. rostratum* (Beddome) Tagawa	TE
86	*Lepidomicrosorium superficiale* (Blume) Li Wang	TE
87	*Lepisorus henryi* (Hieronymus ex C. Christensen) Li Wang	TE
88	*L. macrosphaerus* (Baker) Ching	TE
89	*L. scolopendrium* (Buchanan-Hamilton ex Ching) Mehra & Bir	TE
90	*L. sinensis* (Christ) Ching	TE
91	*L. sublinearis* (Baker ex Takeda) Ching	TE
92	*L. tosaensis* (Makino) H. Itô	TE
93	*Microsorum membranaceum* (D. Don) Ching	TE
94	*Polypodiastrum argutum* (Wallich ex Hooker) Ching	TE
95	*Polypodiodes lachnopus* (Wallich ex Hooker) Ching	TE
96	*Pyrrosia costata* (Wallich ex C. Presl) Tagawa & K. Iwatsuki	TE
97	*P. heteractis* (Mettenius ex Kuhn) Ching	TE
98	*P. laevis* (J. Smith ex Beddome) Ching	TE
99	*P. lingua* (Thunberg) Farwell	TE
100	*Selliguea oxyloba* (Wallich ex Kunze) Fraser-Jenkins	TE
	Pteridaceae	
101	*Haplopteris flexuosa* (Fée) E. H. Crane	TE
	Urticaceae	
102	*Pellionia heteroloba* Weddell	FE
	Zingiberaceae	
103	*Hedychium villosum* Wallich	FE

Abbreviations: TE, True Epiphyte; PHE, Primary Hemi Epiphyte; FE, Facultative Epiphyte